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COMMUNITY MODELS FOR WILDLIFE IMPACT ASSESSMENT: A REVIEW OF CONCEPTS AND APPROACHES

by

Richard L. Schroeder
Resource Evaluation and Modeling Section
National Ecology Center
U.S. Fish and Wildlife Service
2627 Redwing Road
Fort Collins, CO 80526-2899

National Ecology Center
Division of Wildlife and Contaminant Research
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

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PREFACE

Assessments of project-related impacts on wildlife are increasingly using quantified measures to monitor wildlife changes. The use of quantitative measures to assess wildlife impacts has been facilitated by the development of both the Habitat Evaluation Procedures (HEP) (U.S. Fish and Wildlife Service 1980a) and a series of Habitat Suitability Index (HSI) models for a large number of wildlife species (Schamberger et al. 1982). The vast majority of these HSI models have been developed to quantify the habitat needs of individual species. The use of individual species to evaluate habitat and land use changes may not be adequate, however, when information is needed concerning impacts to the entire wildlife community. Consequently, there is a current shift of emphasis, in the Fish and Wildlife Service, to more holistic approaches of performing impact assessments using measures related to the wildlife community.

In a review of the literature related to wildlife community ecology and in discussions with biologists conducting impact assessments, it became apparent that there is a great deal of interest in both the development and use of methods to conduct wildlife assessments at the community level. There are a variety of statements in the literature that allude to a need to manage entire wildlife communities and to prevent the loss of species as functional elements of the ecosystems they occupy (Gottschalk 1975; Maser and Thomas 1977; Odum 1977; Graul 1980; Robbins 1984; Noss and Harris 1986). Unfortunately, the current state of information related to community ecology makes it difficult to understand how specific impacts or management activities affect the entire wildlife community.

The study of community ecology has developed slowly along divergent paths. Ricklefs (1979) identified factors that have hindered development of concepts in community ecology. Specifically, these factors are: the complexity of the subject; difficulties inherent in observation, measurement, and experimentation; divergent viewpoints of ecologists; and the lack of testable hypotheses. Community ecology continues to be a difficult topic to study. There is, nonetheless, a need to incorporate community-level methods in wildlife assessments.

To be most useful, community-level methods should be based on currently accepted ecological concepts, and should allow the quantification of wildlife community features for purposes of comparison and evaluation. There has been, however, relatively little effort, in the field of community ecology, to develop operational methods of performing impact assessments. The purpose of this paper is to provide information on both the concepts and use of community models for wildlife impact assessments, with the objective of improving the understanding of this aspect of applied community ecology.

SUMMARY

The first two sections of this paper are concerned with defining and bounding communities, and describing those attributes of the community that are quantifiable and suitable for wildlife impact assessment purposes. Prior to the development or use of a community model, it is important to have a clear understanding of the concept of a community and a knowledge of the types of community attributes that can serve as outputs for the development of models. Clearly defined, unambiguous model outputs are essential for three reasons: (1) to ensure that the measured community attributes relate to the wildlife resource objectives of the study; (2) to allow testing of the outputs in experimental studies, to determine accuracy, and to allow for improvements based on such testing; and (3) to enable others to clearly understand the community attribute that has been measured.

The third section of this paper describes input variables that may be used to predict various community attributes. These input variables do not include direct measures of wildlife populations. Most impact assessments involve projects that result in drastic changes in habitat, such as changes in land use, vegetation, or available area. Therefore, the model input variables described in this section deal primarily with habitat related features.

Several existing community models are described in the fourth section of this paper. A general description of each model is provided, including the nature of the input variables and the model output. The logic and assumptions of each model are discussed, along with data requirements needed to use the model.

The fifth section provides guidance on the selection and development of community models. Identification of the community attribute that is of concern will determine the type of model most suitable for a particular application. This section provides guidelines on selecting an existing model, as well as a discussion of the major steps to be followed in modifying an existing model or developing a new model. Considerations associated with the use of community models with the Habitat Evaluation Procedures are also discussed.

The final section of the paper summarizes major findings of interest to field biologists and provides recommendations concerning the implementation of selected concepts in wildlife community analyses.

CONTENTS

Page

PREFACE iii
SUMMARY iv
ACKNOWLEDGMENTS vii

CHARACTERIZATION OF COMMUNITIES 1
  Definition 1
  Structure and Function 1
  Community Boundaries 2
QUANTIFIABLE ATTRIBUTES OF THE WILDLIFE COMMUNITY: POTENTIAL MODEL OUTPUTS 5
  Species Richness and Diversity 6
  Wildlife Guild Richness 8
  Species Dominance 9
  Total Wildlife Density and Biomass 9
  Trophic Structure 10
  Community Function 11
  Summary 12
RELATIONSHIP OF INPUT VARIABLES TO POTENTIAL MODEL OUTPUTS 13
  Vegetative Structure 13
  Vegetative Species Composition 14
  Special Habitat Features 15
  Size of Area and Fragmentation 15
  Community Function 16
  Keystone and Indicator Species 17
DESCRIPTION OF EXISTING COMMUNITY MODELS 18
  Habitat Evaluation System 18
  Wildlife Habitat Appraisal Procedure 19
  Stream Corridor Inventory and Evaluation System 19
  Habitat Suitability Index (HSI) Model for Wildlife Species Richness in Shelterbelts 20
  Wildlife Wetland Evaluation Model 21
  Wildlife Species Richness in Wetlands 21
  Habitat Evaluation Index 22
  Arizona Guild and Layers of Habitat Models 22
  Use of Indicator Species to Assess Wildlife Species Richness 23
  Wetland Nutrient and Retention Model 23
  Primary Productivity Model 24
  Summary 24

CONTENTS (Concluded)

Page

APPLICATION OF WILDLIFE COMMUNITY MODELS IN IMPACT ASSESSMENT 26
  Identification of Wildlife Resource Objectives 26
  Guidelines for Selecting an Existing Wildlife Community Model 27
  Modification and Development of Wildlife Community Models 27
  Use of Wildlife Community Models with the Habitat Evaluation Procedures 29
SUMMARY AND RECOMMENDATIONS 31

REFERENCES 33

ACKNOWLEDGMENTS

Community ecology is a complex subject and yet one of tremendous significance to biologists conducting wildlife impact assessments. I have attempted to accurately describe currently accepted concepts of community ecology, while keeping this report readable and reasonably concise. I am grateful to a large number of individuals who, through their excellent reviews, provided invaluable assistance in improving both the technical content and organization of this report.

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CHARACTERIZATION OF COMMUNITIES

DEFINITION

A basic definition of communities is provided by Odum (1971:140): "a biotic community is any assemblage of populations living within a prescribed area or physical habitat." Whittaker (1975:2) defines a community as "a system of organisms living together and linked together by their effects on one another and their responses to the environment they share." Ricklefs (1979) also stresses linkages by defining communities as groups of interacting populations that occur in the same area.

An entire biotic community consists of all of the living organisms, including both plants and animals, within the area of interest. This report focuses on the vertebrate wildlife components (birds, mammals, reptiles, and amphibians) of the entire community, and refers to these components as the wildlife community. Studies of wildlife communities also must consider the plant communities that are present, due to the dependence of wildlife on plants for food and shelter. Although this report primarily discusses terrestrial wildlife, the concepts also apply to fish and aquatic communities.

STRUCTURE AND FUNCTION

Communities consist of groups of populations that have attributes different from individual species or a single population. These attributes can be separated into those that deal primarily with the biological structure of the community and those that deal with community function.

Community structure can be analyzed by assessing either the biological or physical aspects of the community. The biological structure of communities involves species composition and abundance, and the relationships between species (Krebs 1978). Quantifiable measures of the biological structure of wildlife communities include species richness, species diversity, wildlife guild richness, dominance, abundance, biomass, and trophic structure. The physical structure of a community is basically its outward appearance. For example, a deciduous forest has a primary physical structure composed of large deciduous trees and a secondary structure of shrubs and herbaceous growth in the understory. The soil supports the roots of the plants, and the animals of the community distribute themselves within the physical structure provided by the plants and soil. Important components of the physical structure of communities include the growth form of the plants, the vertical stratification or layering of plants, the changes in structure associated with seasonal events, and the horizontal patterns of plant growth.

The physical and biological structure directly affect the functioning of a community (Krebs 1978). Function is the manner in which communities process energy and nutrients. To study the function of communities, one must analyze the food web of the community and then trace the flows of nutrients or energy within the food web. Relationships between measures of community function and the biological structure of the wildlife community are not always clearly understood. Although community ecologists have tended to think of ecosystems from either the biological structure or function viewpoints, neither of these perspectives provides a total description of the system (O'Neill et al. 1986). The biological structure viewpoint tends to consider only certain biotic components of a system and to ignore the functional roles of the biota. The function viewpoint, on the other hand, is concerned primarily with rates of exchange in the entire system, regardless of the composition of the biota. O'Neill et al. (1986) argue that these two viewpoints actually operate as dual hierarchies, alternately imposing constraints on the system.

COMMUNITY BOUNDARIES

Consideration of the location of community boundaries is an important step in both understanding the concept of communities and in conducting impact assessments at the community level. Conceptually, the consideration of community boundaries leads to a discussion of the true nature of communities. Operationally, community boundaries are needed to set limits on the areas to be studied for impact assessment or management purposes.

Community ecologists have tended to have opposing viewpoints on the true nature of communities. Krebs (1978:385) succinctly condensed the controversy in the question "...is the community an organized system of recurrent species or a haphazard collection of populations with minimal integration?" Two opposing lines of evidence, based on studies of plant distribution and abundance, have evolved in response to this dispute.

The superorganism viewpoint, supported by early plant ecologists (Clements 1916; Braun-Blanquet 1931) was that a fundamental unit of communities existed and that the unit itself was natural (not merely a human classification for the sake of convenience). The opposing viewpoint, termed the individualistic view, stressed the importance of vegetational continuity and the individuality of species (Gleason 1926). Several forms of evidence have been presented to evaluate the controversy; much of the evidence favors the individualistic view (Krebs 1978).

The superorganism view of plant communities as discrete, well-defined units lends itself to attempts to classify communities in this manner. Classification of communities into discrete units can be based on a variety of methods, considering such attributes as growth-form dominance, species composition, species dominance, and the structure of the vegetative strata (Whittaker 1975). The location of boundaries will be somewhat arbitrary, depending on the particular method chosen for classification and the users decision as to where to place the boundaries.

The individualistic view of plant communities lends itself to organization using gradient analysis techniques. The statistical orientation of species or communities along a gradient is called ordination. Where gradients exist, ordination techniques may be used to simplify and condense vegetative data in an attempt to show relationships among and between species and environmental variables (Pielou 1969). Use of ordination results in a vegetational continuum without sharp boundaries, and users must choose the manner to distinguish units within the continuum to best meet their interests and objectives.

Although the above discussion considered only plant communities, the concepts apply to wildlife communities as well. Wildlife communities also can be viewed as either discrete units or continuums of many populations. Whereas the concept of a community boundary can be viewed from different perspectives, distinct operational boundaries of communities are necessary to identify the limits of the area of concern and are essential for conducting impact assessments. These boundaries outline the particular location for conducting field analyses. Further, the size of the area within the boundaries is an important determinant of certain attributes of the community, such as the number of species occupying the community.

Operational wildlife community boundaries for impact assessments have often been associated with cover type boundaries of vegetation. Wildlife communities, however, are composed of assemblages of species populations that may or may not have similar distributions in relation to particular groups of plants. It is important to clearly differentiate between the terms community and cover type to avoid confusion and misunderstanding. A community is an assemblage of populations in a given area. A cover type refers to an area of land that contains relatively homogenous vegetation. Whereas the primary purpose of dividing an area into cover types is to facilitate sampling and data interpretation, cover type boundaries also may serve the purpose of delineating the space occupied by the wildlife community of interest. Cover type boundaries, however, are not always the same as the boundaries of the wildlife community of interest. The boundaries of the wildlife community might well include two or more different cover types, or a single cover type might contain several different wildlife communities of interest.

For example, if the wildlife community of interest is all of the vertebrates that use prairie pothole wetlands during the breeding season, the corresponding plant communities to be analyzed should not be limited to wetland cover types. An analysis of wetlands alone would ignore the fact that most species of wildlife that use prairie potholes require both the wetlands and surrounding uplands to meet their habitat needs during the breeding season. The wildlife community boundaries in this example might best be defined to include both wetlands and a surrounding upland zone of a specified width. On the other hand, it is also possible that cover type boundaries may encompass an area larger than that used by the wildlife community of interest. If, for example, the wildlife community of interest was defined as vertebrates restricted to "old-growth" forests, a cover type encompassing all forested areas (including sapling and pole stands) would be much larger than needed. It is important to understand the relationship of the cover type boundaries to the boundaries of the wildlife community of interest.

Determination of boundaries for a taxonomic group of wildlife (e.g., bird community, lizard community, small mammal community) may not accurately represent the extent of the biological relationships that actually exist. A particular difficulty in determining the boundaries of wildlife communities is the mobility of many wildlife species, especially birds. The actual location of operational wildlife community boundaries will involve some level of arbitrariness, because some members of the community will cross any boundary line that is delineated. Careful definition of the wildlife community of interest will lead to the best method to determine the boundaries of the area used by that community.

An additional concern related to determining boundaries is the need to consider the landscape within which the community exists in order to provide the most accurate assessment of overall impacts (Forman and Godron 1986; Noss and Harris 1986). Treatment of communities as isolated entities ignores the possible importance of habitat corridors and juxtaposition of types and their affects on each community. It may be desirable to consider two separate levels of communities when determining boundaries. Impact assessments could then consider both the specific impacts on the primary community affected by an action, as well as the impacts on the larger landscape occupied by the primary community. Noss and Harris (1986) provide an example of this concept, and describe a situation where a small woodlot is of marginal value when considered as an isolated stand, but is actually of high significance when considering its role as an important link in a network of remnant forest patches in an agricultural landscape.

QUANTIFIABLE ATTRIBUTES OF THE WILDLIFE COMMUNITY: POTENTIAL MODEL OUTPUTS

Several attributes of communities can be used as a basis for the development of models for wildlife impact assessments. These attributes generally consider either some aspect of the biological structure of the community or some aspect of community function.

The overall biological structure of a wildlife community may be determined by assessing the number of species in the community and their relative importance. This structure may be portrayed as shown in Figure 1. This figure represents what Whittaker (1965) termed a dominance-diversity curve. The x-axis represents the wildlife species in the community, and the y-axis represents the relative importance of each species. Relative importance is often defined as either abundance or biomass. The curve in Figure 1 [derived from 3 years of bird use data from a Minnesota shelterbelt (Yahner 1980a,b; 1981a,b; 1982a,b)] depicts a typical wildlife community, where a few species are most abundant and the remaining species are represented by a few individuals. Quantified attributes of the biological structure of wildlife communities frequently represent some aspect of a dominance-diversity curve.

Community function is most often described in terms of productivity, energy flow, or nutrient cycling. Quantitative measures of these processes are generally expressed as rates per unit area or per time period. Measures of community function are not easily related to any aspect of the dominance-diversity curve.

The following subsections describe the above quantitative measures of communities, with reference, as appropriate, to the relationship of these measures to the dominance-diversity curve (Figure 1). Each of these measures could be used as an output in a wildlife community model. It is important to note that community level measures of biological structure do not provide information about the presence or status of particular wildlife species, but rather represent a lumping of information to yield a measure at the community level.

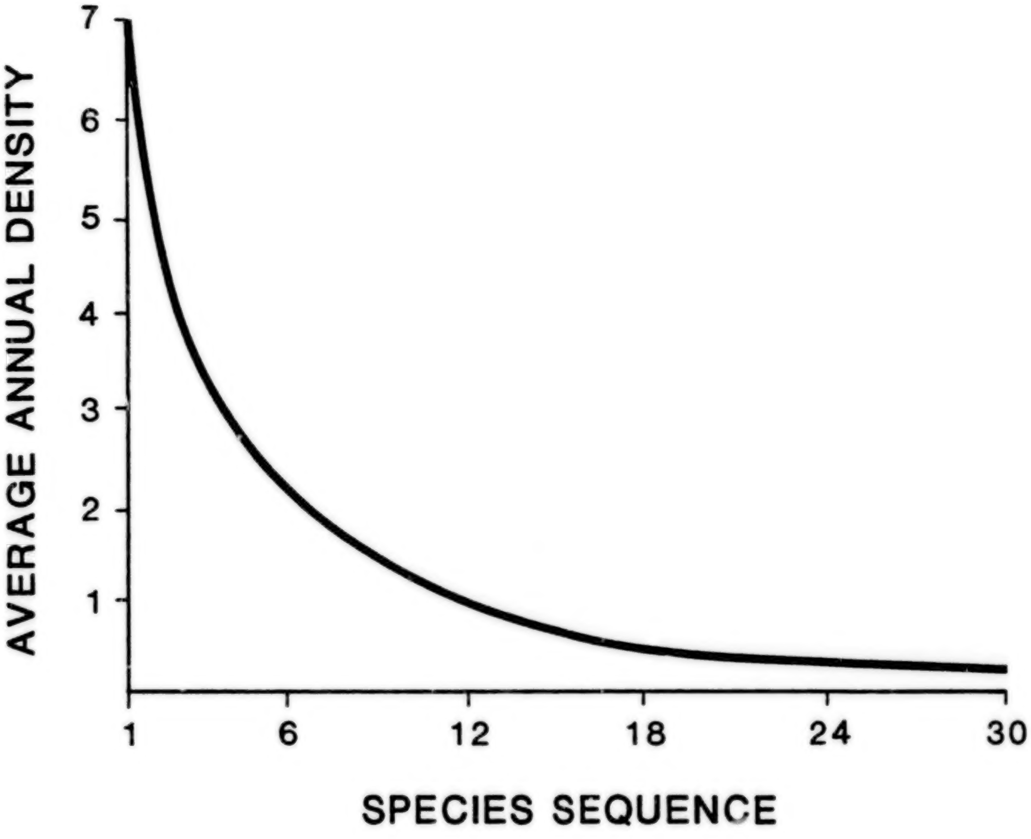

Figure 1. Dominance-diversity curve for a bird community in a Minnesota shelterbelt (based on data from Yahner 1980a,b; 1981a,b; 1982a,b).

SPECIES RICHNESS AND DIVERSITY

Ecologists have sought to develop simple indices of community organization because it is not possible to measure all of the interactions between species in a community (Ricklefs 1979). The most widely studied and used index is species richness, defined as the total number of species in the community (Peet 1974). Species richness is a measure of the length of the x-axis in the dominance-diversity curve (Figure 1).

Species diversity considers both species richness and the equitability of relative importance among the species (Odum 1971). Of the total number of species in a community, only a few are important (many individuals, large biomass, or other indication of "importance"). Ratios between the number of species and the importance values (numbers, biomass, etc.) of the individuals are called species diversity indices, and the use of such indices is extremely widespread in wildlife studies (examples include MacArthur and MacArthur 1961; Kricher 1972; Brown 1973; Dickson 1978; Grant et al. 1982; Yahner 1983a,b; Klein and Michael 1984). Species diversity indices take into account both the length of the x-axis in the dominance-diversity curve and the height along the y-axis for each species. A variety of species diversity indices exist; the most commonly used is the Shannon-Wiener index (derived independently by Shannon and Wiener, and sometimes called the Shannon-Weaver function, Krebs 1978).

The interpetation of diversity index measures is extremely difficult (Whittaker 1972). Although trends in diversity may sometimes be linked to various environmental conditions, higher diversity has no simple relationship to what might be termed environmental "favorableness." A particular difficulty in interpreting species diversity indices is related to the fact that these indices are derived from two components--species richness and equitability. For example, on a tall grass site, grazing caused a sharp reduction in the biomass of two dominant small mammals, which nearly doubled (from 0.42 to 0.82) the evenness component of diversity at the site (Grant et al. 1982). This resulted in an increase (from 0.75 to 1.09) in the diversity index, even though the number of species dropped from 10 to 6. Odum (1969) noted similar difficulties in the interpretation of diversity indices used to describe insect responses to insecticide stresses.

The results of most studies using diversity indices are relatively insensitive to the specific kind of diversity index used, or if just a simple species count is used (Ricklefs 1979). An analysis of bird species diversity based on 267 breeding bird censuses showed that the diversity indices were highly correlated with species richness ($r=0.972$) (Tramer 1969). Species diversity, however, isn't always correlated with species richness, and these two terms are not synonymous (Hurlbert 1971).

Species richness and diversity can be measured for a wide range of different sized areas, either within the boundaries of a single community, across these boundaries, or in large areas encompassing many communities. Measures of diversity within a community are termed alpha diversity (Whittaker 1972). Diversity between communities, defined as the extent of differentiation along habitat gradients, is termed beta diversity. The total diversity of a geographic area, defined as the combination of alpha diversity of the communities and the amount of beta differentiation between communities, is termed gamma diversity. The differences between alpha, beta, and gamma diversity are not always easily distinguished (Peet 1974). For example, many alpha diversity measurements are affected by habitat variation, which could be thought of as beta diversity. Wildlife resource managers have typically emphasized alpha diversity, although beta and gamma diversity are highly relevant to wildlife conservation (Samson and Knopf 1982).

Alpha, or within community, diversity is generally assessed by measures of species richness or species diversity (Whittaker 1972). Several different methods may be used to measure beta diversity (see Whittaker 1972), whereas gamma diversity is generally measured simply as the total number of species in all the available habitats of a fairly large geographic region.

Management for high levels of alpha (within community) diversity has several very significant implications that should be considered by wildlife managers. Maximum alpha diversity may be attained at the expense of loss of species with specific habitat needs that cannot be met under conditions of high alpha diversity (Faaborg 1980; Noss and Harris 1986). In a case study of a tallgrass prairie community, Samson and Knopf (1982) show that management to maximize alpha diversity has little potential to increase or stabilize the distribution of native prairie birds. Increasing alpha diversity in this prairie community would involve increasing vegetational heterogeneity with shrub and tree plantings, providing new habitat for such nonprairie species as brown-headed cowbirds (Molothorus ater) and red-winged blackbirds (Agelaius phoeniceus). Noss and Harris (1986) note that although alpha diversity management increases local levels of species richness, the regional landscape tends to become more homogenous and occupied by more eurytopic species (i.e., species capable of living under a wide range of environmental conditions).

An additional consideration associated with measures of species diversity and richness is that these measures are not sensitive to which species are present in the community. Similar species diversity or richness values in two communities may represent totally different sets of species. The usefulness of these measures may be increased by assessing a particular subset of all species, such as high trophic level species or species occupying the interior of large patches of habitat.

WILDLIFE GUILD RICHNESS

Analysis of a wildlife community also may be accomplished by assessing the richness of groups of wildlife species, referred to as wildlife guilds. A wildlife guild is defined as "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967:335). Wildlife guilds represent species along the x-axis of the dominance-diversity curve (Figure 1) that have similarities in resource use. Guilds have been based on similarities in resource use associated with feeding and breeding strategies of species (Short and Burnham 1982), and on other factors such as species size, habitat preferences, and behavior (Severinghaus 1981). The number of guilds in a wildlife community generally has a positive correlation with wildlife species richness in the community.

The attractiveness of using wildlife guilds for impact assessments is due largely to the fact that there are many fewer guilds than wildlife species; thus, assessments are less time consuming than if each species were considered individually. Further, Short and Burnham (1982) noted that use of guilds allows a more thorough treatment of the entire wildlife community than does the use of selected indicator species. Severinghaus (1981) believed that species occupying the same guild will have similar reactions to any impacts on the resources they share. He stated that "Once the impact on any one species in a guild is determined, the impact on every other species in that guild is known" (Severinghaus 1981:187). The extrapolation of impacts to all guild members, however, is probably not valid (Landres 1983; Szaro 1986). Although species in a guild share a common resource, they each occupy a distinct niche and will vary in their response to a given environmental condition.

A further difficulty in guild analysis is that guilds are arbitrarily defined groupings of species. Guilds may be defined that are extremely general, combining large numbers of species into each guild. Guilds may also be very narrowly defined, so that only a few species share the resources of the guild. The strength of the correlation of wildlife guild richness with community attributes, such as total wildlife species richness, will vary with the level of detail used in guild development. As suggested by Verner (1984) and Szaro (1986), the concept of guild management needs more research and development before it can be recommended as a management tool.

SPECIES DOMINANCE

A small number of species in a community generally exert a controlling influence due to their numbers, size, production, or other actions, and these species or groups of species are known as ecological dominants (Odum 1971). Removal of dominant species from a community would result in more noticeable changes in the community than would removal of nondominant species. Dominance is related to the concept of species diversity, and several indices of species dominance are inversely related to measures of species diversity in the same community (Krebs 1978). Species dominance is related to the few species with the highest importance values along the y-axis of the dominance-diversity curve (Figure 1). A dominance index may be used to monitor changes in the abundance of dominant species, or as an inverse index of species diversity.

TOTAL WILDLIFE DENSITY AND BIOMASS

Total density of individuals or their total biomass per unit area may be used to describe the community. Such measures provide an indication of the standing crop or standing biomass of the entire wildife community. Odum (1971) notes that density tends to emphasize the importance of small organisms, whereas biomass emphasizes the importance of large organisms.

Analysis of data from several studies of bird communities shows that positive correlations may exist between both total bird density and total biomass, and bird species richness (Table 1). Data from a study of small mammal communities in four types of North American grasslands, however, failed to show correlations between total biomass of small mammals and the Shannon-Wiener index of species diversity (H') for these small mammals (Grant et al. 1982).

Assessment of total biomass or density may be made without regard to wildlife species richness. In terms of the dominance-diversity curve (Figure 1), such an assessment would measure the sums of importance values (biomass or density) along the y-axis for all species regardless of the length of the x-axis (number of species). It may be more informative, however, to assess total biomass or density in conjunction with species richness data. Used in this manner, assessments would consider the total length of the x-axis, as well as the sum of heights for all species along the y-axis of the dominance-diversity curve. Subjective judgements would be required to determine the relative desirability of different combinations of total biomass or density and species richness values.

Table 1. Bird density and biomass correlations with bird species richness.

Source	Number of sites	Correlation coefficient (r), bird biomass versus bird species richness	Correlation coefficient (r), bird density versus bird species richness
Karr (1971)	11	0.80(P<0.005)	0.92(P<0.001)
Wiens (1975a)	7	0.77(P<0.05)	0.63(P<0.20)
Wiens (1975b)	70	0.78(P<0.001)	0.76(P<0.001)

TROPHIC STRUCTURE

Organisms within a community may be grouped into various trophic levels, based on whether they are producers, primary consumers, secondary consumers, etc. (Lindeman 1942). Trophic classification is based on function and not on species, because the same species may occupy different trophic levels (Odum 1971). The trophic structure of a community may be measured by assessing standing crop, density, or the energy flow at successive trophic levels. This discussion will consider measures of standing crop and density only; energy flow will be considered in a later section.

Assessments of trophic structure may compare the relative abundance of different trophic levels. Karr (1971) subdivided birds into food-habit categories (insectivore, frugivore, graminivore, omnivore, and carnivore) and determined the percentage of individuals in each category based on their primary foraging strategies. Trophic structure is often used to define wildlife guilds. The foraging portion of the guilds developed by Short and Burnham (1982) subdivides species based on whether they are primary or secondary consumers.

In an analysis of 40 community food webs, Briand (1983) assessed the food chain length of each web as one method to quantify the trophic structure of the community. Food chain length varied considerably, but did not show a significant correlation with species richness in the 40 communities. On the other hand, a measure of the connectance (defined as a direct feeding relation between predator and prey) within the food web matrices was positively correlated with species richness ($r=0.88$, $P<0.001$). In general, the interpretation of measures of trophic structure is difficult. Ecological theory in the recent past held that community stability should increase as the number of links in the food web increased. It has now been shown, however, that there is no simple relationship between diversity and stability in ecological systems (O'Neill et al. 1986).

COMMUNITY FUNCTION

Measures of the rates of various functions may be used as outputs for community models. Such measures describe important processes in the community that cannot be understood by an assessment of the biological structure of the community alone. As noted by O'Neill et al. (1986), ecosystems are probably regulated by alternately imposed constraints related to either the function or biological structure of the system. Whereas the following ecosystem functions undoubtedly serve important regulatory roles in ecosystems, their relationship to the biological structure of the community is not always clear.

Primary productivity is the rate at which plants assimilate the energy of sunlight. Primary production generally provides the foundation for the entire trophic structure of the community, and both energy flow and nutrient cycling through communities are linked to the primary productivity of plants. In terrestrial ecosystems, primary production is determined largely by light, temperature, and rainfall, and is generally measured by estimating the annual increase in plant biomass. Productivity is likely the most significant single attribute of a natural community (Whittaker 1975). All biological activity in a community depends on the energy of primary productivity.

The presence of both food-producing and food-consuming organisms in a community creates a structure through which energy flows and nutrients cycle, called the trophic structure (Ricklefs 1979). As energy flows through various levels of the trophic structure, from primary producers to high-level consumers, most energy is dissipated and lost through heat or motion. Thus, the amount of energy passed between trophic levels always becomes smaller with each passage. The efficiency of movement of energy through a community is determined by the efficiency with which organisms exploit and convert food resources into biomass.

The total flow of energy and the efficiency with which it flows determine the basic structure of a community (Ricklefs 1979). Measurement of energy flow through an entire community, however, is complicated and virtually impossible. Regardless of the method used to define community boundaries for study purposes, energy often moves in and out of the community across these boundaries. Both the strength and weakness of the use of energy flow in community analysis is that it allows the combination of different species and reduces the diversity of a community to a single unit of measurement--the calorie (Krebs 1978).

Nutrients, unlike energy, are continually recycled between living organisms and the physical environment (Ricklefs 1979). The assimilation and decomposition processes that cycle nutrients are closely linked to the energy flow in a community. Nutrients reside in compartments, which are any defined space in the community, such as all plants, a single species of plant, or a plant part (Krebs 1978). The rate of movement of nutrients between compartments and the quantity of nutrients in each compartment define the nutrient cycle. Nutrients may cycle locally within a community or globally through the atmosphere. Rates of nutrient movement are more important in determining ecosystem structure and function than the amount of nutrients present in a system at any one time (Odum 1971). Nutrient cycling studies are very time consuming, and complete studies are practical only for long-term research (Westman 1985).

SUMMARY

The preceding section describes several quantifiable attributes of communities that may be used in wildlife impact assessment studies. The use of quantitative measures of either the biological structure of the wildlife community or community function has several important implications that must be understood prior to conducting a community-level wildlife assessment.

A significant problem in the use of measurements of biological structure occurs when they are used simply as descriptive statistics, with no reference to important ecological questions or hypotheses (Alatalo 1981). For example, there is little value in calculating a specific diversity index unless the information it yields is useful in terms of what is needed to understand the community (Hurlbert 1971). The fact that a particular diversity index may show a correlation with a property of the community does not indicate that the index is either appropriate or useful. Another important characteristic of structural measures at the wildlife community level is that they are not sensitive to which species exist in the community. Two communities may have similar values for a particular measure, but yet contain very different sets of species. For example, in a study of bird habitat use in the Lower Colorado River Valley, Rice et al. (1984) found that the average bird species richness varied only slightly between years, while the actual bird species composition changed greatly.

Christensen and Peet (1984) note that proper management depends on the identification and understanding of the structural and functional features of the species within the community. The current level of knowledge in the field of community ecology, however, makes such "proper" management extremely difficult to accomplish. It is difficult to understand the interrelationship of measures such as species richness, biomass, species dominance, energy flow, and nutrient cycling. O'Neill et al. (1986:186) agree and note that "Simply stated, the problem is that the relationship between organisms in a system and the functions of the system is not always clear." The use of a particular community level attribute as a model output should be based on as clear an understanding as possible of its relevance to the problem at hand.

RELATIONSHIP OF INPUT VARIABLES TO POTENTIAL MODEL OUTPUTS

This section describes input variables that may be used in community models, and notes how these variables are thought to be related to the various community attributes (potential model outputs) described in the previous section. Much of the information is taken from studies of avian habitat use. As noted by Rice et al. (1984), such studies have strongly influenced ecological theory.

VEGETATIVE STRUCTURE

The physical structure of vegetation plays a major role in determining the nature of the wildlife community in a given area. Vegetative structure can be measured in a variety of ways, but the most commonly used measures are related to either the horizontal or vertical complexity of the vegetation within a habitat. MacArthur and MacArthur (1961) measured the foliage height diversity (FHD) of eastern deciduous forests and found that FHD was positively correlated with bird species diversity (BSD). FHD was calculated by assessing the amount of foliage in each of three vertical layers of the forest and is basically a measure of vertical stratification. Positive correlations between FHD and BSD also have been shown in other studies (Karr and Roth 1971; Willson 1974), although this relationship may not exist in all situations (e.g., Tomoff 1974).

The horizontal structure of vegetation also affects BSD. The percent canopy cover of vegetation in Illinois habitats was positively correlated with BSD (Willson 1974). Roth (1976) found a strong positive correlation between a measure of horizontal vegetative patchiness and BSD in shrub habitats in Illinois and Texas. However, BSD was not found to be correlated with a measure of habitat heterogeneity in North American grasslands (Wiens 1974).

The number of lizard species in western North America was shown to be positively correlated with a measure of plant volume diversity (based on three volume categories for small shrubs, large woody shrubs, and trees) (Pianka 1967). Rosenzweig and Winakur (1969) found a positive correlation between the number of small mammals in desert habitats and an index of habitat complexity (based on the vertical and horizontal complexity of the vegetation and soil structure). Short (1984) discussed the relationship of wildlife species richness and the vertical structure of vegetation in a variety of Arizona habitats. Analyses of Short's data show that bird species richness is positively correlated with the number of vertical layers of vegetation, whereas the number of species of mammals or reptiles and amphibians show no such correlation. It appears that measures of vegetation structure within a habitat are most useful for predicting avian community attributes. The relationship of vegetative structural complexity to other wildlife groups has not been clearly demonstrated.

It is not necessary to restrict measures of vegetative structure to a single plant community type. Vegetative structure measured across several plant community types may be used to assess wildlife diversity at the beta (between habitat) level. Samson and Knopf (1982), in an analysis of data from Salt (1957), measured beta diversity for birds in three major vegetative communities in Wyoming (coniferous forest, deciduous forest, and wetlands). They concluded that management directed at increasing alpha diversity would favor birds that are ecological generalists, whereas management to increase between-habitat diversity (beta diversity) would favor birds that are more restricted in their habitat use and would promote gamma level diversity.

VEGETATIVE SPECIES COMPOSITION

The species composition of vegetation has a direct affect on the number and types of wildlife species that occur in a given area. Tomoff (1974) found that plant species composition was highly significant in determining breeding bird community structure in desert scrub habitats. The presence of a few key plant species with distinctive growth forms provided nest sites for a large number of bird species.

MacArthur and MacArthur (1961) noted that the correlation between FHD and BSD was not improved with the addition of plant species diversity to the regression formula. They concluded that habitats with similar values for FHD will have the same BSD values, regardless of the number of plant species. Recent analyses of bird communities along the Colorado River, however, have shown that many birds are strongly influenced by tree species compositon (Rice et al. 1984). Rice et al. (1984) believe that the reason FHD is correlated with BSD is likely due to the accumulation of different patches of habitats with different plant species. The interrelationship between vegetative structure and plant species composition is clearly stated by Holmes et al. (1979: 518):

> "... bird community composition within and between forest habitats is largely dependent on the physical structure of the vegetation, the kinds and distribution of foraging substrates, and the availability and abundances of insect resources, all of which are influenced by the species composition of the plant community. The change in species composition and growth form of plants along a height gradient within a forest provides differing combinations of foraging opportunities that ultimately determine how many bird species can occupy that environment."

A review of individual species habitat models shows that many species of mammals also prefer certain vegetative species composition. Examples include the preference for hard mast tree species by the gray squirrel (Allen 1982), spruce-fir (Picea-Abies) forest preferences of the marten (Allen 1984), and specific plant species forage preferences of the white-tailed deer (Short 1986). The relationship of plant species composition to the entire mammalian wildlife community, however, has not been well documented.

SPECIAL HABITAT FEATURES

Many wildlife species or groups of species require special habitat features to ensure their presence. For example, it has been shown that decreasing the availability of snags will cause decreases in the density, diversity, and species richness of cavity nesting birds (Balda 1975). Cavity nesting birds composed approximately one-third of the total numbers of breeding birds in a ponderosa pine (Pinus ponderosa) habitat, and snag removal reduced the number of cavity nesters by 57%. Cavities in snags are also used by a wide variety of mammals. Thus, snags are a special habitat feature that strongly influence the overall wildlife community in forested habitats.

Many raptors have needs for special habitat features, such as cliffs, tall trees, or cavities in trees, to meet nest site requirements (Olendorff et al. 1980). The presence of these and other special habitat features will help to ensure that raptors will exist in an area. Raptors are high on the food chain and are valuable to the maintenance of the community they occupy (Balda 1975). In addition, raptors are key indicators of the effects of ecologically disruptive activities (Olendorff et al. 1980).

Management solely for the special habitat needs of a few species or groups of species may have negative impacts on other species in the community (Graul and Miller 1984). Special habitat features probably should be used to complement other community approaches.

SIZE OF AREA AND FRAGMENTATION

The relationship of the number of species to the size of an area has significant implications in the study of wildlife communities. This relationship was explored on islands (MacArthur and Wilson 1967) and later extended to interior habitat (Galli et al. 1976; Martin 1978; Robbins 1979). The general equation given by MacArthur and Wilson (1967) to express the species-area relationship is:

$$S = cA^z$$

where S = number of species

c = a constant that depends on the taxon and geographic region

A = area

z = a constant measuring the slope of the line relating S and A

In the eastern and north-central forests of the United States, there are several bird species that depend on large, extensive forest systems for their continued survival (Whitcomb et al. 1981; Robbins 1979, 1984). Recent fragmentation of these large forests, due to urban sprawl, highways, reservoirs, etc., has caused a reduction in the numbers of birds species. Robbins (1984) noted a reduction in the number of neotropical migrant bird species in forests less than 1,700 ha in size. The large-area needs of carnivorous mammals such as mountain lions (Felis concolor), wolves (Canis lupus), and grizzly bears (Ursus arctos) must be considered to maintain complete faunal assemblages (Harris 1984). Based on the requirements of large carnivorous mammals, there is also a need to develop a system of connecting corridors between suitable large habitat islands (Harris 1985). Management without concern for the size of the area carries a high risk of eliminating area-sensitive species (Graul and Miller 1984).

Habitat patch size and connectedness have direct effects on the frequency and persistence of localized extinctions (Fahrig and Merriam 1985). Isolated populations of white-footed mice (Peromyscus leucopus) had higher probabilities of local extinctions, and reestablishment of populations took longer in isolated habitat patches than in connected ones.

Species-area relationships do not account for the minimum critical size of ecosystems needed to maintain natural communities over long periods of time (Lovejoy and Oren 1981). It is important to consider impacts to functioning ecosystems and their processes, and not just assess the numbers of species. However, this is not easily accomplished; many important questions related to critical ecosystem size remain to be answered. Noss and Harris (1986) address this issue by recommending the integration of individually important communities through the establishment of a system of interconnecting corridors over very large geographic areas. Such an integrated system would encourage movement of species, nutrients, energy, and changes in habitat patches, across space and time. These processes would help to facilitate gene flow among populations and help to insure the long-term survival of wide-ranging wildlife species.

COMMUNITY FUNCTION

Measures of community function may serve as input variables as well as outputs in community models. Productivity of primary producers in a community limits the size of animal populations in the system (Westman 1985). It has been suggested that increased productivity causes increases in species diversity, but evidence concerning this hypothesis is contradictory. Connell and Orias (1964) support the hypothesis and state that increased productivity during succession should support increased wildlife diversity. Gauthreaux (1978), using data from Whittaker (1975) and Tramer (1969), suggested that more productive forests have greater numbers of bird species. A positive relationship between productivity and the number of common desert rodent species (Brown 1975) is one of only a few empirical demonstrations of this hypothesis (Giller 1984). Conversely, neither the abundance nor biomass of breeding birds in cental Illinois was correlated with the annual productivity of the community (Willson 1974). Primary productivity in Danish lakes was inversely correlated with the diversity of crustacean consumers (McNaughton and Wolf 1973). Other studies have also shown inverse correlations between productivity and diversity (Grice and Hart 1962; Margalef 1969; Whiteside 1970, all cited by Whittaker 1972). It is probable that primary productivity and species diversity are not correlated in most terrestrial plant communities (Whittaker 1972) and bear no simple or intrinsic relation to one another (McNaughton and Wolf 1973; Giller 1984).

Available energy entering a community does not necessarily determine the production of a given species or trophic level in terrestrial systems (Wagner 1969). Production of consumers may be limited by a variety of factors, which must be understood in order to make predictions about the impact of a change in the environment of a community (Krebs 1978). Krebs (1978) believes there is not a single community for which this level of understanding exists. Analysis of nutrient cycling may have important implications for solving environmental problems (Ricklefs 1979). A disruption of a step in the nutrient cycling process, reinforced through successive cycles, may lead to instability in a community. Nutrient depletion and eutrophication are examples of problems caused by such disruptions. As stated earlier, however, the relationship between measures of community function and the biological structure of the community are not always clear (O'Neill et al. 1986).

KEYSTONE AND INDICATOR SPECIES

A keystone species is one which exerts a controlling influence over the biological structure or functioning of a system. This concept was developed by Paine (1966) in studies of intertidal systems. Removal of keystone species from a system may result in changes in the rates of ecosystem functions (O'Neill et al. 1986). Examples of possible keystone species include whales, elephants (O'Neill et al. 1986), lobsters (Krebs 1978), and a starfish (Paine 1974).

The concept of indicator species is similar to keystone species, but somewhat more general. The term "indicator" is loosely used to describe species whose presence or abundance is viewed as representative of other desired features of the community. Various rules or logic for selecting indicator species have been proposed by several authors (Graul 1980; Szaro and Balda 1982; Robbins 1984; Wilcox 1984). These rules describe features, such as stenotropism, high trophic level, large body size, and large area requirements as useful for the identification of indicator species. None of these rules, however, are supported by empirical data that clearly link the indicator species with particular community attributes.

The utility of using keystone or indicator species as inputs in a community model is directly related to how well the selected species' role in the system is understood. In situations where the species' role is clearly known, this approach may serve to simplify a community-level analysis. This level of understanding, however, does not often exist.

DESCRIPTION OF EXISTING COMMUNITY MODELS

This section provides a brief review of several currently available models that may be useful in assessing impacts to wildlife communities. A general description of each model is provided, along with information on the geographic area and community types to which it applies. The nature of the output for each model is noted, and input variables are briefly described. Following the descriptions, a quick-reference matrix is provided as well as summary comments concerning use of existing models.

HABITAT EVALUATION SYSTEM

The Habitat Evaluation System (HES) (U.S. Army Corps of Engineers 1980) was developed for use in assessing wildlife communities in most aquatic and terrestrial habitats of the Lower Mississippi Valley. The terrestrial evaluations are based on four major plant community types: wooded swamps, bottomland hardwood forests, upland forests, and openlands. The basic approach of HES is to assign values from 0 to 1 for a variety of vegetative and landscape variables and to combine these indices for several variables in a community type by using a relative weighting factor and summing the weighted indices. The final overall value for a community type is termed the Habitat Quality Index (HQI). The specific meaning of the HQI is ambiguous, and is defined in the text as being "a function of the general value of a habitat for wildlife populations." It appears that many of the variables are intended to estimate wildlife species richness. However, reference also is made to relationships to wildlife species diversity, and to habitat values for game species such as waterfowl, turkey, and white-tailed deer.

A maximum of eight input variables are required to compute an HQI for each community type. The majority of these input variables require detailed site-specific data, such as percent ground cover, percent understory cover, and the number of trees larger than specified diameters. The text of HES contains brief statements explaining the logic for assigning values from 0 to 1 for each input variable; however, most of these statements do not have documented sources. No explanation is provided for the rationale used to weight and combine input variables to produce the HQI output.

The bottomland hardwood forest portion of HES is currently being revised and updated and will be available in late 1987 (T. Pullen, U.S. Army Corps of Engineers, Vicksburg, Mississippi; pers. comm.).

WILDLIFE HABITAT APPRAISAL PROCEDURE

The Wildlife Habitat Appraisal Procedure (WHAP) was developed to assign a Biological Habitat Component score to various plant community types found in Texas (Frye 1984). These community types are based on the physiognomic structure of the vegetation or substrate. The model output (0 to 1) is derived from the sum of weighted values for components related to soil productivity, vegetative structure and diversity, and scarcity of the community type. The components that are measured are those that "contribute to the ecological condition of the evaluated tract and resulting overall suitability for wildlife." The assumptions listed in the text imply that the output is related to wildlife species diversity and population densities of wildlife species. The output, however, is not clearly defined.

The WHAP primarily considers measures of alpha diversity, such as vegetative complexity and soil type within the community. One variable considers the uniqueness and scarcity of the community type, which is a measure related to gamma diversity. The values of all variables, however, are summed for the final score, which confounds the interpretation of this score related to alpha or gamma diversity concepts. This procedure assesses the same components in each community type, and, given the assigned values for specific categories of each component, it appears that maximum scores can only be obtained in mature bottomland hardwood stands. A community type such as climax prairie would yield a score about one-third the maximum obtainable in a bottomland hardwood stand.

Site-specific data are required to use the WHAP model. Most of the criteria, however, are general in nature and would not require detailed or time-consuming field sampling. For example, criteria for upland habitats require determination of the number of woody plant species, ocular estimates of vegetative height in one of three categories, and ocular estimates of whether or not canopy coverage in each category exceeds 25%. Several of the criteria contain subjective wording, including such phrases as "readily apparent" and "occurring infrequently." The procedure requires data for only seven components, and the author notes that the procedure was developed to allow wildlife habitat evaluations without requiring a significant amount of field work or data compilation. The WHAP model does not include documentation of the sources of information used in the selection of the components and their weighting factors.

STREAM CORRIDOR INVENTORY AND EVALUATION SYSTEM

The Stream Corridor Inventory and Evaluation System (SCIES) is a method for determining the value of stream corridors to wildlife (Garcia et al. 1984). Stream corridor boundaries are identified by the user; the text provides several examples of possible classification methods. The criteria used to assess terrestrial wildlife habitat along streams are designed to yield high values in areas with the potential to support large numbers of species and high densities of individuals. Criteria were selected that possess "strong predictive capabilities for a wide spectrum of wildlife." The SCIES approach subdivides terrestrial habitats into eight guild habitat units, based on vegetative and topographic conditions. Several parameters are evaluated for each guild habitat unit, and the parameter values are weighted and combined to provide a single value for each guild unit. The guild units also are weighted and combined to provide a single overall value for the terrestrial habitat. There are a large number of very detailed parameters that must be weighted and combined, but the system provides no defined weights for the parameters, nor any specific logic for developing weights. The recommended method for assigning relative weights is through a committee process, using the judgement of persons familiar with the wildlife community of interest. Although this approach is flexible, it is also likely to be arbitrary and not repeatable. Documentation of the system states that the output is related to species richness and density, but the flexibility of the system leaves the meaning of the output unknown, unless it is defined by the persons selecting the parameters and weights.

Detailed, site-specific data are needed to run the SCIES model. Forty-five parameters are suggested to determine a value for terrestrial habitat along a stream corridor, and many of these require detailed site measurements of features such as foliage volume, snag size, and plant species diversity. Several of the parameters may be assessed from remotely sensed data or obtained from existing data sources. The SCIES model includes detailed documentation for the sources of information for each parameter.

HABITAT SUITABILITY INDEX (HSI) MODEL FOR WILDLIFE SPECIES RICHNESS IN SHELTERBELTS

The HSI model for wildlife species richness in shelterbelts (Schroeder 1986) was developed for use in the northern Great Plains. The model output is an index value ranging from 0 to 1, with 1 representing an individual shelterbelt with maximum wildlife species richness and values approaching 0 representing successively lower levels of wildlife species richness. The model is based on measures of vegetative structure, plant diversity, and the size of the shelterbelts.

There are six input variables in the model, five related to the vegetation and one to the size of the shelterbelt. The five vegetative variables are tree height, canopy closure, number of rows and their configuration, and number of woody plant species. The output is highly sensitive to changes in either vegetative conditions or the size of the shelterbelt. The model yields an HSI value for each shelterbelt under consideration. Guidance is provided regarding methods that might be used to apply the model to determine a single value for species richness for many shelterbelts.

The HSI model for shelterbelts provides detailed documentation of the sources of information used in the development of the model. The model output was shown to have a positive correlation ($r=0.86$, $P<0.05$, $n=7$) with year-round bird species richness in Minnesota shelterbelts.

WILDLIFE WETLAND EVALUATION MODEL

A model to evaluate wildlife values in freshwater wetlands of the northeastern United States was developed by Golet (1976). The output of the model is a value between 36 and 108, with higher values intended to indicate high levels of both wildlife diversity and wildlife productivity. A detailed wetland classification system identifying 26 wetland classes and subclasses is provided in the model. The classification system separates wetlands based on differences in plant structure and water regime.

The model is based on 10 criteria related to vegetative composition and structure, wetland size, interspersion, and water chemistry. Each criterion is subdivided into five specific ranks and assigned a weighting factor. The overall score is determined by summing the weighted rankings for all criteria in the wetland. Documentation of the source of information is provided for several of the criteria; however, the logic and rationale for their ranks and weighting factors is not well documented. Most of the data needed for this model can be obtained from remote sensing and wetland classification sources.

Although this model is intended to predict both species diversity and wildlife productivity, the author acknowledges that these two characteristics are not strictly compatible. It would be difficult to interpret whether particular model outputs reflect the diversity or production component.

WILDLIFE SPECIES RICHNESS IN WETLANDS

A model to predict year-round levels of wildlife species richness for wetlands in the 48 conterminous States of the United States was developed by Adamus (1983), as a part of a much larger document that assesses a variety of wetland functions. The procedure recommends classifying wetlands according to the system developed by the U.S. Fish and Wildlife Service (Cowardin et al. 1979). This model is based on a key that yields a qualitative output of high, medium, or low for wildlife species richness, and is intended to compare these levels only within wetlands of the same system type.

Important components of the key include wetland size, gradient, configuration, vegetative diversity, vegetative interspersion, and human disturbance. Each component contains general descriptive categories (for example, wetland size <2 ha or >80 ha), and wetlands are rated on the basis of whether the majority of the components meet the desired condition. Many of the descriptive categories provide a broad range of possible conditions within each category, and many descriptions are subjective in nature. Data are required for over 25 components, some of which would require detailed site measurements and others that could be obtained from remotely sensed or existing data. A very general level of documentation is provided to justify the inclusion of most components; however, the rationale for combining the components into a rating of high, medium, or low is not provided.

HABITAT EVALUATION INDEX

The Habitat Evaluation Index (HEI) (Graber and Graber 1976) was developed to evaluate the biological richness of communities across the entire State of Illinois. Communities were classified into 23 types based on plant species composition, growth form, and age (for example, willow-cottonwood, 30-59 years old). Three factors contribute to the index: the replacement time for a community type, the scarcity of the community type, and the changing availability of the community. These factors are combined for each community type in a study area, and then summed for all types. This sum is compared with the average condition in the State to yield the HEI.

The authors state that the HEI is related to the biological richness of the study area, but this relationship is not documented in the text. The index is most likely related to the gamma (regionwide) level of species richness. Due to the nature of the weighting factors used, an area with community types that are structurally simple but scarce Statewide, such as native prairie, may have higher HEI's than an area with structurally complex forest types that are more abundant Statewide. Thus, although alpha richness is higher in the forests, the prairie has a higher HEI due to its scarcity at the gamma level. This relationship is not always true, however, because the HEI may also vary between communities with similar levels of regional scarcity, but different replacement times. Thus, interpretation of the HEI for several community types would be difficult.

Computation of the HEI is straightforward, but the data in the model are restricted to Illinois. Prior to application in other States or regions, data would need to be compiled on areas, replacement times, and changing availability of the proposed community types. Once this was accomplished, application would require mapping and area computations for the locations of interest, as well as a minimal amount of field work.

ARIZONA GUILD AND LAYERS OF HABITAT MODELS

The Arizona guild and layers of habitat models (Short 1984) were developed to evaluate the structural complexity of habitats in southwestern desert and riparian habitats. The basic concept of these models is that the vertical dimension of vegetation is important in determining the number of wildlife species in a community (Short 1984). The guild model places wildlife species into a species-habitat (guild) matrix based on the foraging and nesting location of each species. The model predicts a Habitat Suitability Index (HSI) value based on a comparison of the amount of each area and the potential number of guilds in each area with the number of guilds that would be present if the total area consisted of the most structurally complex community, in this case the riparian treeland.

The layers of habitat model assumes that wildlife species richness will increase with increases in the number and area of vertical habitat layers. The model defines eight vertical habitat layers based on vegetative height and density, and the presence of water. The number of wildlife guilds (based on vertical partitioning of the habitat) is, as would be expected, positively correlated ($r=0.99$, $P<0.01$, $n=13$) with the number of habitat layers.

Computation of an HSI for the guild and layers models assumes that an ideal condition is represented by the most structurally complex community. Such a comparison assumes that alpha species richness is desired, and does not consider the contribution of some structurally simple plant communities to beta and gamma levels of wildlife species richness.

The guild and layers models were developed for 13 plant communities within the Sonoran Desert, classified according to both plant structure and plant species composition. Use of these models within the Sonoran Desert consists primarily of mapping the communities and determining their size. Application in new areas, however, would require determination of the number of wildlife guilds and habitat layers for all communities of interest.

USE OF INDICATOR SPECIES TO ASSESS WILDLIFE SPECIES RICHNESS

The U.S. Forest Service and Colorado Division of Wildlife developed one of several approaches that utilize indicator species to assess wildlife species richness (Hoover and Wills 1984). This approach assumes that management for a few carefully selected indicator species will ensure the presence of all other species in the community. Seventeen forest communities in Colorado are identified based on plant species composition, and habitat requirement information is provided for 70 vertebrate wildlife species that occupy these communities. Based on an assessment of the habitat needs of the selected indicator species, forests are managed so that indicator species populations are maintained at ≥20% of their assumed maximum attainable population levels.

Although general guidelines are provided on how to select indicator species, the final selection is left to the user with the advice to choose enough species "to be representative of the habitat requirements of all the species in the management unit" (Hoover and Wills 1984:36). Therein lies the difficulty in using indicator species to assess an entire wildlife community. It is very difficult to know which subset of species will best indicate overall wildlife species richness levels within a community.

WETLAND NUTRIENT AND RETENTION MODEL

Adamus (1983) developed keys to predict relative levels of nutrient retention and removal in freshwater wetlands. The keys assume that the following factors are important in determining levels of nutrient cycling in wetlands: hydroperiod, sediment-trapping effectiveness, substrate, vegetation type, and current velocity. The keys provide only a subjective output of high, medium or low, and do not equate these terms with any specific nutrients or quantified rates of cycling. Adamus (1983) states that the effectiveness of the keys is lowered due to the complicated and poorly understood chemical, vegetational, and physical interactions within wetlands.

PRIMARY PRODUCTIVITY MODEL

Cantilli et al. (1978) proposed a very general method that can be used to determine the changes in primary productivity caused by land use changes. Estimated rates of primary productivity are provided for several major community types (tropical forest, temperate forest, boreal forest, etc.) and are used to determine the direct energy loss caused by alteration or removal of a community type. The degree of an impact is assessed by comparing the energy losses in each community type for various alternatives, and determining whether changes in the trophic structure of the system will be caused by the energy loss.

This system provides an estimate of changes in primary production with major changes in land use, but is not useful for analyzing impacts within a community type that is not changed to another type by the impact of a project. The method provides no linkage to wildlife values, and, although trophic structure is mentioned, no guidance is provided to analyze the effects of changes in primary productivity on trophic structure. The primary productivity rates are apparently global averages; Lieth (1975) notes that regional productivity estimates are more important for land use planning.

SUMMARY

The models reviewed above are representative of the types of community models used for wildlife impact assessment and management purposes. Various other models are available; reviews of additional models are contained in Harker et al. (1981), Roberts and O'Neil (1983), and Lonard et al. (1984).

The summary matrix of models versus model inputs and outputs (Table 2) reveals some interesting points. The majority of these models have an output related to wildlife species richness or diversity, generally at the alpha level. None of the model outputs are directly related to other wildlife community attributes, such as species dominance, biomass, density, or trophic structure. A review of the literature related to models used for wildlife impact assessments revealed no models with these outputs.

Further, it can be seen that most model inputs are related to vegetative structure, species composition, and the size and fragmentation of the communities. None of the models directly use inputs of community functions, such as productivity, energy flow, or nutrient cycling. Even though these community functions may be important in their effects on the wildlife community, it appears that these relationships are not clearly understood. In addition, the high cost of gathering such data precludes their use in most assessment studies.

A common characteristic of many of the wildlife community models is the lack of a clearly defined and testable output. Outputs on the matrix that have a "?" indicate that the model does not clearly define the output, and thus, the output is subject to considerable interpretation. The lack of clearly defined outputs is a serious weakness in these models, because it makes it impossible to validate the model and difficult to communicate with others about what is being measured in the wildlife community.

Table 2. Matrix of community models versus model inputs and outputs. (Note: a "?" denotes a model output that is implied, but not clearly defined.)

Model inputs and outputs	Habitat Evaluation System (U.S. Army Corps of Engineers 1980)	Wildlife Habitat Appraisal Procedure (Frye 1980)	Stream Corridor Inventory & Evaluation System (Garcia et al. 1984)	Shelterbelt HSI Model (Schroeder 1986)	Wildlife Wetland Evaluation Model (Golet 1976)	Wildlife Species Richness in Wetlands (Adamus 1983)	Habitat Evaluation Index (Graber & Graber 1976)	Arizona Guild & Layers of Habitat Models (Short 1984)	Indicator Species/ Species Richness (Hoover & Wills 1984)	Wetland Nutrient Model (Adamus 1983)	Primary Productivity Model (Cantilli et al. 1978)
INPUTS:											
Vegetative structure	*	*	*	*	*	*		*	*		
Vegetative species composition	*	*	*	*	*	*	*		*	*	*
Special habitat features	*	*	*			*				*	
Size/fragmentation	*		*	*	*	*	*				
Community function measures											
Keystone or indicator species									*		
OUTPUTS:											
Alpha species richness or diversity	?	?	?	*	?	*			*		
Wildlife guild richness								*			
Gamma species richness							?				
Species dominance											
Total species density											
Total species biomass											
Trophic structure											
Primary productivity											*
Energy flow											
Nutrient cycling										*	

APPLICATION OF COMMUNITY MODELS IN WILDLIFE IMPACT ASSESSMENTS

IDENTIFICATION OF WILDLIFE RESOURCE OBJECTIVES

An essential first step prior to selecting, developing, or using a community model is to develop clearly stated wildlife resource objectives. Without a clear statement of objectives, it is difficult to determine the type of model needed. An important consideration in setting wildlife resource objectives is to distinguish between ecological relationships and human value judgements (see Powell 1982). The choice of a specific objective reflects human value judgements concerning the desired features of a community or ecosystem.

Wildlife assessments at the community level may be directed at several possible objectives. Examples of specific objectives for community assessments include the following:

- Attain desired population levels of a particular assemblage of vertebrate species. In his studies of grassland birds, Graul's (1980:40) goal was to "maintain all general grassland types so that no existing avian species is lost as a functional element of its respective ecosystem."

- Attain desired levels of wildlife species richness or diversity within a community. This goal is explicitly stated or implied in a wide variety of wildlife studies and assessment procedures. Balda (1975) described such an application as attempting to produce the maximum number of species at density levels that most closely reflect natural conditions.

- Attain desired levels of wildlife species richness or diversity across several communities or in a large geographic region.

- Attain desired levels of other community attributes, such as total density, total biomass, or a measure of community function.

It is important to consider the scale of the study when wildlife species richness or diversity are a part of the objectives. For example, an objective to maximize species richness within the community (alpha scale) would require a model quite different than an objective to maximize species richness across a large region (gamma scale). Another important consideration related to objectives for species richness or diversity is to consider the issue of native versus exotic species. Measures of total species richness and diversity do not account for what species are present, and it may be desirable only to consider the needs of the native wildlife community.

Following the determination of wildlife resource objectives, potential model outputs related to these objectives should be identified. Outputs should be selected that will serve to assess whether or not progress is being made toward reaching the stated wildlife resource objective. Depending on the nature of the objectives, it may be difficult to decide on a community attribute that will successfully measure progress toward their attainment. For example, consider Graul's (1980) goal to maintain species as functional elements of their ecosystem. This goal sounds very appealing and is likely a high priority for many resource managers. However, the phrase "functional element" is vague and would need to be further defined before it could be adequately assessed with a specific model output. It appears that a serious problem in the application of wildlife community models is the lack of clear objectives that can be tracked quantitatively with specific model outputs. The importance of this point cannot be overemphasized.

GUIDELINES FOR SELECTING AN EXISTING COMMUNITY MODEL

Existing models should be carefully reviewed to determine their potential utility for application in a specific study. The most important guideline for selecting an existing model is to determine if the model output will be useful in monitoring progress toward study objectives. The geographic region and community types to which the model applies should be considered in assessing the utility of the output.

Another important consideration in selecting a model is related to the data and sampling requirements of the model. These requirements will directly influence the time and cost required to conduct the analysis. Consideration should be given to the availability of existing data with which to conduct the study, compared to the amount of data that must be collected. The sampling requirements necessary to obtain adequate data must be within the range of time, money, and experience available to the user.

A clear understanding of the assumptions and limitations of a model is essential in determining whether or not the model will be useful in addressing the wildlife resource problems of concern. A few models have detailed and explicit explanations of their assumptions and limitations, while many are somewhat vague in explaining these factors. Users must understand these assumptions and limitations and should decide if they are acceptable prior to using a specific model. Understanding the assumptions and limitations of a model will also help users who wish to attempt to modify the model for site-specific applications.

MODIFICATION AND DEVELOPMENT OF COMMUNITY MODELS

Users are faced with two choices when existing community models do not meet their needs: modify an existing model or develop a new model. Model modification will most likely be less time consuming than development of an entirely new model; however, the basic steps to be followed are identical. These steps are essentially the same as the phases of HSI model construction outlined by the U.S. Fish and Wildlife Service (1981), and are briefly summarized below.

The first step is to set the model objectives related to both the model output and the geographic area of applicability. As already stressed, model outputs should address the resource problems of concern and serve to track progress toward meeting the overall wildlife resource objectives.

The second step requires the identification of input variables to be used in the model. Input variables that are commonly used in wildlife community models were reviewed in an earlier section of this paper. Users should select from these and other significant variables and determine which variables are the best predictors of the specified model output. This is facilitated in step three, where the model is structured and input variables are combined to yield a single, quantitative output. A large number of possibilities exist for methods to combine input variables, too numerous to discuss in detail in this report. Again, users are referred to the HSI model guidelines of the U.S. Fish and Wildlife Service (1981) for more information.

The final two steps of model modification or development are critical to the successful understanding of the model and its behavior. The fourth step involves documentation of the data sources and information used to develop model hypotheses, along with detailed explanations of the known assumptions and limitations of the model. This information is vital in helping others to understand the logic structure of the model and useful when future modifications are required.

Model verification is the final step and involves, at a minimum, analysis of model behavior using a variety of real or hypothetical data sets. The purpose of these analyses is to insure that the response of the model to a given set of inputs is compatible with the model builders' perceptions. The data sets used should approach the limits of the model, within the bounds of what would be expected in real world situations. Ideally, the model will be developed with enough real data to allow some calibration of the model output. Unfortunately, information on outputs, such as total wildlife species richness, and inputs, such as vegetative structure, is not always available.

The following example briefly discusses the development of the shelterbelt HSI model (Schroeder 1986), with reference to data availability for alternative models. The shelterbelt HSI model yields an output related to wildlife species richness in individual shelterbelts of the northern Great Plains. The input variables are measures of vegetative structure, plant species composition, and the size of the shelterbelt. The selection of input variables and the combination function used to derive a single output were strongly influenced by detailed studies of bird communities conducted by Martin (1978) and Yahner (1983a,b). In addition, quantified bird data collected over a 3-year period in Minnesota shelterbelts (Yahner 1980a,b; 1981a,b; 1982a,b) were used in correlation analyses to modify the structure of the model and to verify its utility. A limitation of the shelterbelt HSI model is that it is only applicable to individual shelterbelts. The model does not predict total species richness for multiple shelterbelts distributed over a large area. Efforts to expand the capabilities of the model to cover this situtation proved futile, due to a lack of data from which to develop reasonable hypotheses.

Development or modification of wildlife community models may be difficult in situations where inadequate data exist to meet the defined wildlife resource objectives. Users are encouraged to follow the suggestion of Graul and Miller (1984:288) and "emphasize the strengths of several approaches, perhaps combine some, and modify them as new information becomes available." In addition, it may be helpful to seek the advice of experts with knowledge of the wildlife communities of concern.

USE OF WILDLIFE COMMUNITY MODELS WITH THE HABITAT EVALUATION PROCEDURES

The Habitat Evaluation Procedures (HEP) (U.S. Fish and Wildlife Service 1980a) is an accounting system that is used to quantitatively compare changes in habitat values as a result of management actions or project impacts. Habitat quality in HEP is usually determined with the use of a model, most frequently for individual species of wildlife. The accounting unit in HEP is the habitat unit (HU), defined as the product of habitat quality (expressed as a 0 to 1 index) and habitat quantity. There are a few important considerations that should be addressed prior to using a wildlife community model in the HEP accounting system.

It is assumed in HEP that the HU is based on a ratio number. This concept implies that an increment of change in HU's is equal to the same increment of change in the wildlife community attribute being measured, at any level of possible HU values. For example, doubling an HU value implies a doubling in the amount or quality of the wildlife attribute of interest. Care must be taken to insure that the wildlife attribute being measured will fit the criteria of being a ratio number. Use of the Shannon-Wiener diversity index (H'), for example, may cause difficulties. It might not be acceptable to assume that doubling H' results in a situation two times more desirable from a wildlife community perspective. As explained earlier, H' is sensitive to changes in both species richness and the evenness of species distribution. Therefore, it may be difficult to interpret the meaning of HU values computed if species diversity (H') is used as the index of habitat quality.

The relationship of species abundance measures (species richness or diversity) to area causes additional difficulties in a typical HEP analysis, when the 0 to 1 value determined for a wildlife community is multiplied by area to determine habitat units (HU's). Area is then considered twice, confounding the interpretation of the meaning of specific HU values. If the wildlife assessment considers species richness or diversity for each discrete physical area occupied by the wildlife community of interest, it is implied that many small sized areas can have richness or diversity values greater than one or more much larger areas. Depending on the vegetative conditions within the areas, the distances between the areas, and other factors, this may or may not be true. Schroeder (1986) discusses this problem in the shelterbelt HSI model and concludes that the best alternative may be to develop a model that predicts species richness for the combined number of discrete areas occupied by the wildlife community of interest. If this were done, the model output would directly consider area, and would not need to be multiplied by area for HU determination. The model output alone could be the equivalent of a typical HU value for use in HEP. Development of a model to predict species richness or diversity for the combined areas occupied by the wildlife community of interest would be difficult. Development of such a model would require data on the interrelationships between variously sized and spaced areas and their component wildlife communities. Data such as these are difficult to obtain. Given the lack of available data, the alternative is to develop a model based on reasonable hypotheses. The general structure of such a hypothetical model has been developed to predict overall tree species richness for scattered patches of forest stands in southeastern Wisconsin (Rudis and Ek 1981).

SUMMARY AND RECOMMENDATIONS

In the review of the literature related to community models for wildlife impact assessments, several major findings are noteworthy. There is a great deal of interest in both the development and use of models to conduct wildlife assessments at the community level. Various statements in the literature allude to a desire to manage entire wildlife communities and to prevent the loss of species as functional elements of the ecosystems they occupy. Unfortunately, the current state of information related to community ecology makes it difficult to understand the complexities of the structure and function of wildlife communities and how management activities affect structure and function within a community. Although there are several community models available, the ecological implications of using a specific model are not always clear.

Many measures of the biological structure of wildlife communities result in a single output, such as an index of species diversity. The desire to understand and evaluate wildlife communities through such single outputs is understandable, yet it creates many difficulties. The majority of these indices represent a combination of two or more distinct community attributes, and thus, are misleading. For example, it is very difficult to interpret the ecological meaning of an index that is related to both species richness and equitability, or one that is a measure of diversity and productivity. A constant value of the final index may reflect many different values of its component parts.

The majority of the models that were reviewed (see Table 2) assess either alpha species richness or alpha species diversity. Very few models consider richness or diversity at the beta or gamma levels, and none had outputs indicative of species dominance, biomass, density, or trophic structure. The predominance of models with outputs related to species richness or diversity reflects the perceived importance of these attributes. This also is indicated by various policies and legislation of various government entities. The National policy of the U.S. Fish and Wildlife Service for fish and wildlife habitat management states that "the Fish and Wildlife Service shall encourage the management of ecosystems for species diversity" (U.S. Fish and Wildlife Service 1982). The National Forest Management Act (90 Stat. 1949; 16 U.S.C. 1600) requires the Secretary of Agriculture to develop guidelines for land management planning on National Forest lands that provide for diversity of plant and animal communities (Peterson 1984).

Although it has been stated that measures of community function, such as energy flow and nutrient cycling, may be the desired methods of impact assessment (Ricklefs 1979; U.S. Fish and Wildlife Service 1980b; Westman 1985), the relationship of these measures to wildlife populations is often unknown. Several site-specific, research-oriented studies of community function exist, but very few operational techniques are available to implement these concepts in wildlife assessments. Direct measures of community function are extremely time consuming.

Conceptually, a community model can be envisioned that recognizes the importance of both the functional and structural attributes of the system. Such a model could have several intermediate outputs related to function and structure that are then integrated in a manner that accounts for alternately imposed limits on the system. Development of such a model, however, is limited by our understanding of these relationships. Further, application of such a model would likely be extremely time consuming. Therefore, given the current levels of understanding related to wildlife community ecology and acknowledging the perceived importance of considering species richness or diversity, I make the following recommendations.

The concept of management of species richness at the gamma level should be further incorporated into current assessment activities. Maximizing species richness at the alpha (within community) level may have detrimental effects on the number of species across a broad geographic area (gamma level). Implementation of this concept would be assisted by a "top down" approach to community assessment. A "top down" approach would identify local areas that are essential to the maintenance of gamma species richness and could provide a framework for fitting local decisions into a larger regional perspective.

The relationship between species richness and area should receive additional consideration in wildlife community assessments. As pointed out by Harris (1985), many large vertebrate species require very large areas to ensure their survival. In situations where individual areas are too small for the maintenance of these very large vertebrates, connecting corridors between a mosaic of communities may be required. Many neotropical migrant bird species also require large areas before they use a site for nesting (Robbins 1984). Rather than using total species richness as a model output, consideration should be given to assessing the species richness of "core" species (species that are restricted to the interior of large patches, see Temple 1986).

Forman and Godron (1986) describe the emerging field of landscape ecology and discuss the importance of considering the entire landscape in environmental assessments. Important landscape features include the size of patches of different plant communities, the shape of patches, patch configuration, connectivity, and the flow of species, energy, and nutrients through the landscape. Noss and Harris (1986) provide a practical example of a suggested application of these concepts in north Florida and south Georgia. They illustrate how a number of currently isolated parks and refuges could be linked together through the use of riparian and coastal corridors.

The incorporation of these concepts into wildlife community assessments appears to hold great promise for ensuring the protection of a wider variety of species than typically occurs. These concepts, however, have not yet been formulated into practical, workable models with quantified outputs. It appears that the task at hand is to recognize the importance of considering both the structure and function of wildlife communities within the landscape they occupy and begin development of working models to facilitate these efforts. The point is not to abandon species analyses, but rather to add more levels in the biological hierarchy to impact assessment and management activities.

Despite the advances in theoretical ecology in recent years, a major task of applied ecology is to make environmental assessments more of a science than an art (Krebs 1978). Krebs (1978:608) summarizes our current condition very well:

> "The message of ecology today is essentially one of very great complexity, and the problems ecologists are attempting to analyze are as formidable as any in science. We must recognize this complexity but try not to take shelter in it. Most of the ideas of ecology are still hypotheses with an unknown range of applicability. These hypotheses do have consequences, and the job of ecologists must be to translate these hypotheses into practical suggestions."

A variety of techniques and procedures already exist that attempt to incorporate ecological hypotheses into working tools for impact assessment and management purposes. It is the job of managers and decisionmakers to make the best use of available information to meet their wildlife resource objectives. As noted by Bender et al. (1984), it is important to remember that ecological techniques must be supplemented by a large amount of descriptive natural history and common sense. The increased interest in wildlife community assessment reflects a growing desire to assess our actions from a perspective broader than that of individual species. Throughout these efforts, users are encouraged to proceed with caution. A critical factor in the use and acceptance of community level approaches to impact assessment and management is a clear understanding of their strengths and weaknesses in meeting specific wildlife resource objectives.

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This document provides a review of the concepts and approaches associated with the use of community models in wildlife impact assessments. Quantitative attributes of wildlife communities that may serve as model outputs are identified. Key vegetational, spatial, and functional input measures are described. Brief descriptions are provided for a variety of existing wildlife community models. Information is included on the application of wildlife community models on impact assessments. A final summary reviews noteworthy findings and includes recommendations for incorporating the findings into current impact assessment efforts.

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42

TAKE
PRIDE IN
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Preserve Our Natural Resources

DEPARTMENT OF THE INTERIOR
U.S. FISH AND WILDLIFE SERVICE

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43

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